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EVIDENCE THAT ION REGULATION IN HYDROMEDUSAE AND CTENOPHORES DOES NOT FACILITATE VERTICAL MIGRATION

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Abstract

Medusae and ctenophores, like many types of gelatinous zooplankton, actively exclude sulphate ion from their mesogloeal body fluid and thus gain lift (buoyancy). It is hypothesized that vertically migrating species might show day/night variations in the rate of sulphate elimination to regulate buoyancy dynamically and that such changes are a major factor in vertical migration. To test this hypothesis, a series of laboratory experiments were conducted using medusae and ctenophores. Concentrations of radioactive sulphate were measured in equilibrium (uptake) experiments and concentrations of sodium, magnesium, potassium, and calcium ions were measured using atomic absorption spectrophotometry. No evidence of day/night (light/dark) changes in ion concentrations were found for the hydromedusae *Aequorea victoria, Aglantha digitale, Gonionemus vertens, Mitrocoma cellularia, Phialidium gregarium, Polyorchis penicillatus, Sarsia tubulosa,* and *Stomotoca atra* or for the ctenophore *Pleurobrachia bachei.* It is concluded that changes in ionic regulation are not a major factor in diel vertical migration. It is thus hypothesized that for these animals vertical migration is accomplished solely by swimming.

Introduction

Jellyfish, like many planktonic organisms, are often restricted to relatively narrow depth ranges in the sea. These distributions may be modified diurnally for species that undergo vertical migrations, moving toward the surface at night and into deeper water during the day. One of the most impressive vertical migrations of a hydromedusa is that of *Solmissus albescens* in the Adriatic Sea (Benović, 1973). This jellyfish, which is usually less than 3 cm in diameter, moves up and down more than 300 m each way daily. The hydromedusa *Aglantha digitale* performs the most extensive vertical migration among the jellyfish in the Puget Sound—Strait of Georgia region where the present work was done, moving up and down as much as 100 m each way daily (Arai and Fulton, 1973; Mills, 1982).

In order to maintain themselves consistently at certain depths, planktonic animals must either attain neutral buoyancy, somehow balancing the weight of their proteinaceous tissues, or they must establish swimming routines to overcome buoyancy differentials. Most hydromedusae in the Puget Sound—Strait of Georgia region are not neutrally buoyant. At rest in surface waters, most species sink approximately 20–120 cm per minute (Mills, 1981 and unpub. obs.). Only a relatively small number of the local species of hydromedusae are either neutrally or positively buoyant. Of

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the negatively buoyant species, most have intermittent swimming patterns of short duration that serve both to maintain a given depth in the water column and simultaneously to facilitate feeding (Mills, 1981).

The mesogloea, or jelly, of a hydromedusa is a highly hydrated, acellular fibrous material. Several studies have shown that the concentrations of major ions in cnidarian mesogloea are generally similar to sea water, with one major exception—the concentration of sulphate ion within the mesogloea is much lower than in the surrounding sea water (Macallum, 1903; Koizumi and Hosoi, 1936; Robertson, 1949). Chloride concentration in the mesogloea is somewhat higher than in sea water, apparently as a result of the isosmotic replacement of sulphate ions by chloride ions (Robertson, 1949). The work of Robertson (1949) and Mackay (1969) suggests that excretion of sulphate ion (along with associated cations) in jellyfish is accomplished by an active transport system across the epithelium.

Elimination of sulphate from the body fluids of gelatinous planktonic organisms provides buoyancy. Denton and Shaw (1962) and Bidigare and Biggs (1980) have calculated that partial elimination of sulphate ions and isosmotic replacement with chloride provides enough lift to balance some or all of the relatively heavy proteinaceous tissue. For example, Bidigare and Biggs (1980) found that in the ctenophore *Beroe cucumis,* elimination of 55% of the sulphate relative to sea water provides 1.2 mg of lift per ml of mesogloeal volume, offsetting all of its protein mass and rendering this weak swimmer neutrally buoyant. The more robust scyphomedusa *Pelagia noctiluca* eliminates 38% of the sulphate relative to sea water, gaining 0.8 mg of lift per ml of mesogloeal volume and offsetting only 66% of its protein mass; unlike *Beroe, Pelagia* is a strong swimmer and has no difficulty in overcoming its residual negative buoyancy by active swimming. Thus sulphate elimination may either completely or only partially offset the heavy components in a jellyfish. The final buoyancy is apparently the result of morphology (amount and distribution of heavy and buoyant tissues) and a trade-off between energy used in swimming and that used in sulphate elimination.

Given that a low sulphate concentration in the mesogloea is maintained by an active transport system, the question arises as to whether vertically migrating medusae can diurnally vary the rate of sulphate elimination, thereby facilitating vertical migration by actively regulating buoyancy. It has not yet been established whether vertical migration of medusae is accomplished solely by swimming, or solely by regulation of buoyancy, or by a combination of both mechanisms (Mackie, 1974). Extensive observations of hydromedusae in a 1500 l aquarium (Mills, 1981, 1983) however, have not revealed any visible changes in buoyancy between day and night. Thus, if buoyancy is regulated diurnally, the magnitude of change may be insufficient by itself to drive migration; on the other hand, even a small change in buoyancy would facilitate swimming.

The purpose of the present paper is to test empirically the hypothesis that sulphate concentration in jellyfish varies on a day/night basis in such a way that vertical migration might be facilitated. Accordingly, we have determined the concentrations of sulphate and of several other ions in whole medusae and have compared values for animals held in the light and dark. Measuring ions other than sulphate served as a secondary method for investigating possible day/night ion-controlled buoyancy changes, since concentration changes of any ion are expected to be accompanied by changes in one or more counterions in order for the jellyfish to remain in osmotic equilibrium with sea water. In previous experiments (Mills, 1983), it was established that rhythms of vertical migration in medusae are responses to light and dark rather than to intrinsic clocks. That is, medusae held in continuous light (or dark) for long periods continue to behave appropriately for that light condition. Subsequent changes

in lighting elicit abrupt changes in migratory behavior which are appropriate to the new light condition.

Materials and Methods

Animals

In all experiments it was considered of paramount importance that the medusae be in excellent condition and that they be handled as little as possible during the experiments. Most of the animals were collected individually in beakers from the floats in front of the Friday Harbor Laboratories. *Gonionemus* medusae were collected by the same procedure in Mitchell Bay, San Juan Island, Washington, and *Polyorchis* medusae were collected from Shoal Bay, Lopez Island, Washington, and from Bamfield Inlet, British Columbia. Animals were always collected during the day and had always experienced at least 8 hours of light prior to being placed in the dark. Medusae were gently transferred to larger containers of sea water and were maintained under a regulated light regime in an 11°C walk-in coldroom at the Friday Harbor Laboratories. Experiments were begun within a few hours of collection.

To test the ion regulation/vertical migration hypothesis, species representing various diel behavior patterns (Mills, 1982) were selected for this study. *Aglantha digitale* is a long-range vertical migrator that moves as much as 100 m each way daily. *Gonionemus vertens* lives in bays only a few meters deep, but nevertheless has a pronounced migration, spending the daytime mostly attached to vegetation on or near the bottom and spending the night swimming near the surface. *Polyorchis penicillatus* also lives in shallow bays, but does not exhibit such a pronounced vertical migration. *Polyorchis* medusae swim up and down all the time, but they seem to spend more time near the surface at night. *Stomotoca atra, Phialidium gregarium,* and *Aequorea victoria* all tend to remain in the uppermost 25 meters. Here *Stomotoca* appears to make a short-range vertical migration; *Phialidium* apparently makes a short-range reverse vertical migration (moving down at night); and *Aequorea* shows no evidence of a day/night pattern. *Pleurobrachia bachei* apparently migrates upward within the upper 50 m at night. Diel behaviors of *Mitrocoma cellularia* and *Sarsia tubulosa* are not known.

Sulphate protocol

Sulphate concentrations of whole medusae were investigated using radioactive sulphate ($Na_2{}^{35}SO_4$) in order to establish whether the concentrations of sulphate attained under light *versus* dark conditions were different. The following six species of hydromedusae were incubated in natural sea water plus 40–200 μCi/l of $Na_2{}^{35}SO_4$ in constant light or in constant dark as described in Table I: *Gonionemus vertens, Mitrocoma cellularia, Phialidium gregarium, Sarsia tubulosa, Aglantha digitale,* and *Aequorea victoria.*

Shortly after collection, medusae were transferred to small paper cups or glass beakers containing natural sea water plus labeled sulphate. For 4 of the 6 species, some medusae were left under a fluorescent room light and others were placed in a dark drawer in the same room. All *Aglantha* and *Aequorea* medusae were left in the light because only small numbers of these animals were available.

Medusae in the light were sampled intermittently to establish equilibrium values for each species (Fig. 1). Sulphate concentrations in *Sarsia* and *Aequorea* did not equilibrate during the experimental period (45 and 76 hours, respectively) and sampling was terminated when the remaining individuals began to look unhealthy. Medusae

TABLE I

Conditions of radioactive sulphate saturation experiments for 6 species of hydromedusae held in constant light or constant dark

Species name	Length of experiment (hours)	Time to equilibrate (hours)	$\mu Ci^{35}SO_4$ per liter SW	# medusae per volume SW	Wet weight of single medusae (g)
Gonionemus vertens	66	≤20	66	2/75 ml	0.220–1.186
Mitrocoma cellularia	109	≤85	40	2/500 ml	1.00–2.74
Phialidium gregarium	45	≤8	66	2/50 ml	0.086–0.463
Sarsia tubulosa	45	≥45	66	2/50 ml	0.054–0.360
Aglantha digitale	54	≤4	200	2/50 ml	0.017–0.155
Aequorea victoria	76	≥76	200	1/75 ml	0.874–3.300

Time to equilibrate was determined from plots of sulphate concentrations in Figure 1.

which had been kept in the dark were analyzed only at the final time point for medusae of the same species held in the light, for the purpose of comparing light *versus* dark sulphate concentration at that time. Each medusa was removed from the labeled sea water, carried through 2 rinses of fresh sea water, blotted "dry" on a paper towel for 5–15 seconds depending on the species, and then was homogenized through a 20-gauge syringe needle into a preweighed vial. Each vial was immediately capped and reweighed to determine the wet weight of the medusa. In order to determine the amount of radioactive sulphate remaining in each container, two 0.5 ml samples of radioactive water were taken to accompany each medusa, and were placed in separate vials. Three ml of Aquasol scintillation fluid (New England Nuclear, Inc.) were added to all vials. All samples were counted for 5 minutes on a Beckman LS8000 liquid scintillation counter using a broad C^{14} window. Radioactive counts ranged between 2000 cpm (in *Gonionemus* and *Mitrocoma*) and 40,000 cpm (in *Phialidium*). Values were not adjusted for quenching. Radioactivities of the medusae relative to the sea water, after adjustment for the blotted wet weights of the medusae, were then calculated as cpm per ml of jellyfish divided by cpm per ml of sea water. Student's *t*-test was used to compare light and dark mean values at the final time point for all species except *Aglantha* and *Aequorea* (for which no dark values were determined due to a shortage of animals).

Sodium, magnesium, potassium, and calcium protocol

Concentrations of sodium, magnesium, potassium, and calcium ions in whole medusae maintained in either light or dark were measured using a Varian AA-475 series atomic absorption spectrophotometer. Ten individuals each of 6 species of medusae (*Aequorea victoria, Gonionemus vertens, Mitrocoma cellularia, Stomotoca atra, Polyorchis penicillatus,* and *Phialidium gregarium*) and of one ctenophore (*Pleurobrachia bachei*) were carefully hand collected and transferred into 500–1000 ml beakers (5 medusae per beaker) in an 11°C walk-in coldroom. Medusae were collected in late morning or early afternoon and then held in fluorescent light until mid-afternoon when all had experienced 10–14 hours of "daylight." At this time, for each species, one-half of the animals were placed in a dark drawer and one-half remained in the light. After 2 hours, both sets of medusae were processed as follows. Each medusa was picked up gently with forceps and blotted "dry" on a paper towel for 5 to 15 seconds, depending on the species. The whole medusa (or in the cases of

Aequorea, Mitrocoma, and *Polyorchis,* where the animals were large, ¼ of a whole medusa was used) was then placed in a preweighed glass scintillation vial and the weight of the medusa was recorded. Four 1.0 ml sea water samples were also taken for comparison. One ml of analytical grade nitric acid was then added to each vial in order to dissolve the medusa, and the vials were capped with polyethylene-lined lids. Some of the samples required gentle heating on a hotplate for about 20 minutes to dissolve fully the animal tissue.

For A.A. spectrophotometric measurements, the dissolved medusae were diluted to 100 ml (and secondarily diluted up to 500 ml where necessary) in volumetric flasks using ultrapure water from a Sybron/Barnstead NANOpure filter with measured conductivity less than 7.0 megohms/cm. Standard solutions were made up using ultrapure water as follows: 20, 100, 200 ppm sodium; 2, 10, 20 ppm magnesium; 0.8, 4, 8 ppm calcium; and 0.8, 4, 8 ppm potassium. Sodium and potassium were measured from emission, and magnesium and calcium were measured from absorption. Concentrations of these ions were converted from ppm (μg/ml of sample) to μg/g wet weight of jellyfish. The ion concentrations in the jellyfish were subsequently compared to ion concentrations in Friday Harbor sea water (ppm in the animal $\times$ 100 divided by ppm in sea water) in Figures 3–6.

Results

Sulphate

Sulphate concentrations are shown for 6 species of hydromedusae (Fig. 1). The concentration in *Gonionemus vertens* appears to have equilibrated within about 20 hours, with a tissue sulphate concentration equivalent to 8% of the concentration in the external sea water. *Mitrocoma cellularia* had apparently equilibrated by 85 hours, containing an average of 24% of the external sulphate although no intermediate points were taken for this species. *Phialidium gregarium* appears to have equilibrated in less than 10 hours, containing an average of 77% of the external sulphate. *Sarsia tubulosa* also had not obviously reached equilibration by 45 hours when sampling of this species was terminated because the animals were beginning to look unhealthy; at that time they contained an average of 27% of the external sulphate. *Aglantha digitale* had apparently equilibrated by the time the first samples were taken at 4 hours, containing an average of 28% of the external sulphate. *Aequorea victoria* had not obviously reached equilibration by 76 hours, when it contained 87% of the external sulphate.

Sulphate levels in both light and dark were obtained for all of the above species of hydromedusae except *Aglantha* and *Aequorea.* Mean light and dark values for each species are plotted in Figure 2. For *Gonionemus, Mitrocoma, Phialidium,* and *Sarsia,* two-tailed *t*-tests show no significant difference in sulphate uptake levels in continuous light *versus* levels in continuous dark.

Sodium, magnesium, potassium, and calcium

Mean ion concentrations in whole animals (6 species of hydromedusae and 1 ctenophore) after 2 hours in the light or after 2 hours in the dark are shown in Table II and Figures 3–6. Although the 10 individuals of each species were of various sizes, the standard deviations were very low. Student's *t*-test failed to reveal significant differences in any case between ion concentrations in the light and after 2 hours of darkness.

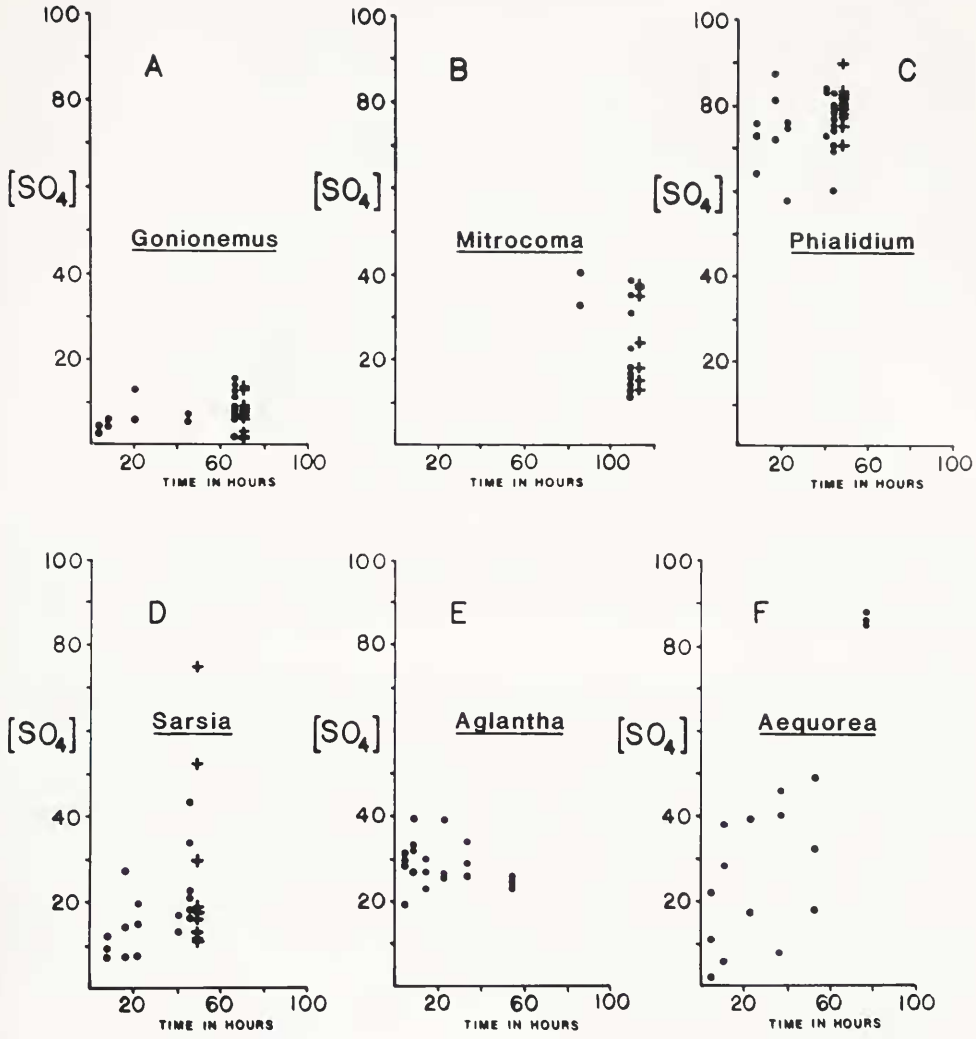

FIGURE 1. Uptake of sulphate ($Na_2{}^{35}SO_4$) in 6 species of hydromedusae in constant light (●) or dark (+). Sulphate levels are expressed as specific activity of the medusa (cpm/ml) × 100 divided by specific activity of the sea water (cpm/ml). (A) *Gonionemus vertens,* (B) *Mitrocoma cellularia,* (C) *Phialidium gregarium,* (D) *Sarsia tubulosa,* (E) *Aglantha digitale,* (F) *Aequorea victoria.*

DISCUSSION

Within the sensitivities of the methods used, there is no evidence for a general phenomenon of light/dark (day/night) variation in the concentrations of sulphate, sodium, magnesium, potassium, or calcium ions in the hydromedusae and ctenophores examined. In nature, it is dark for only 4 to 5 hours during mid-summer when these studies were conducted. Medusae migrate upward shortly after dusk and downward at dawn, so any useful change in buoyancy should be indicated during the first hour of darkness or light. Although the radioactive sulphate experiments necessarily occurred over an unnaturally long period of uninterrupted light or dark, agreement of these

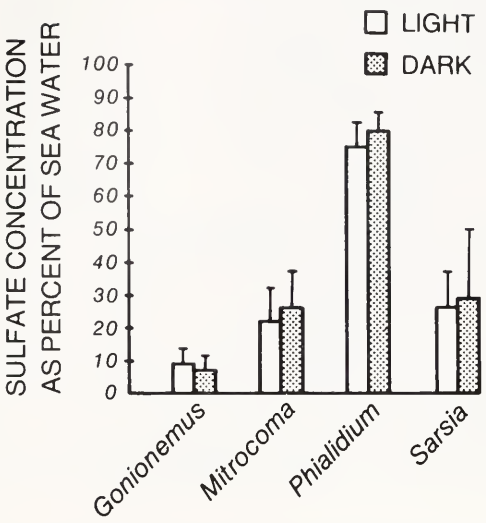

FIGURE 2. Sulphate concentrations of 4 species of hydromedusae in the light and dark relative to sulphate concentrations in sea water. Each bar represents the mean of 6–12 samples (see Figure 1 for precise sample sizes). One standard deviation is indicated above each bar.

results with the more realistic light/dark time periods used for medusae in which other ion concentrations were determined lends strength to the former studies. Since the five measured ions do not vary between day and night, it is implied that probably no ions vary substantially between day and night, because one would expect that change in one ion should be balanced by an opposing change in one or more other ions. Furthermore, it is unlikely that, if ionic movements are involved in producing day/night differences, other cations are involved, because with the exception of ammonium, all major sea water cations were checked. It is conceivable that an anion other than sulfate might be actively transported, creating density differences over the 24 hour cycle, but no examples of buoyancy regulation by anions other than sulphate are known, so this possibility is rather remote.

TABLE II

Ion concentrations in whole medusae after approximately 15 hours of light (L) or after 2 hours of darkness following approximately 13 hours of light (D)

Species	Wet weight (g)	Sodium (μg/g)		Magnesium (μg/g)		Calcium (μg/g)		Potassium (μg/g)	
		L	D	L	D	L	D	L	D
Aequorea victoria	3.756–6.598	9414	9308	1054	1051	485.2	493.8	429.2	382.4
Gonionemus vertens	0.659–1.187	8170	7797	666.5	673.4	332.2	333.6	1418	1491
Mitrocoma cellularia	2.906–4.548	9469	9502	988.2	965.6	436.2	425.4	652.2	649.4
Phialidium gregarium	0.163–0.517	9665	9747	1017	1041	442.6	447.8	426.4	427.6
Polyorchis penicillatus	1.411–4.552	8777	8633	943.8	943.2	515.0	527.8	1313	1213
Stomotoca atra	0.249–0.573	9280	8970	800.5	825.4	444.5	444.2	653.2	655.0
Pleurobrachia bachei	0.521–1.083	9284	9221	969.4	976.6	464.8	417.6	439.8	426.8
Sea water (1 ml)	1.028–1.051	9326		1216		471.0		355.0	

Values given are the means of 5 samples; standard deviations are shown in Figures 3–6.

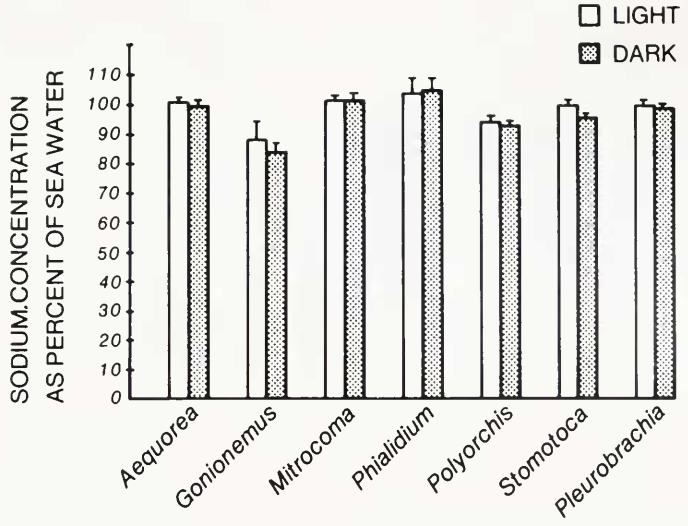

FIGURE 3. Sodium concentrations of 6 species of hydromedusae and 1 ctenophore in the light and dark relative to sodium concentration in sea water. Each bar represents the mean of 5 samples. One standard deviation is indicated above each bar.

The species of jellyfish used in this study represent a diverse set of diel behavior patterns (see *Animals* above). Since day/night ion concentrations in medusae do not vary in accordance with diel activity patterns, it is postulated that vertical migration is apparently accomplished by swimming and not by diel ionic regulation of buoyancy. Alternatively, it is conceivable that diel changes in feeding could allow the use of gut contents to function as a buoyancy factor for vertical migration. *Phialidium, Mitro-*

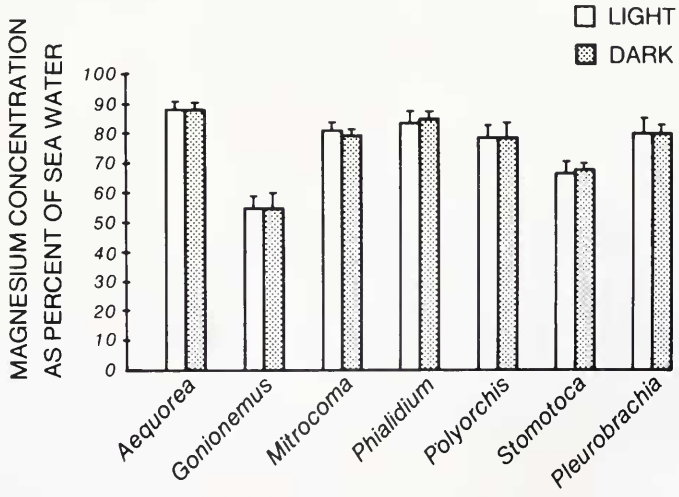

FIGURE 4. Magnesium concentrations of 6 species of hydromedusae and 1 ctenophore in the light and dark relative to magnesium concentration in sea water. Each bar represents the mean of 5 samples. One standard deviation is indicated above each bar.

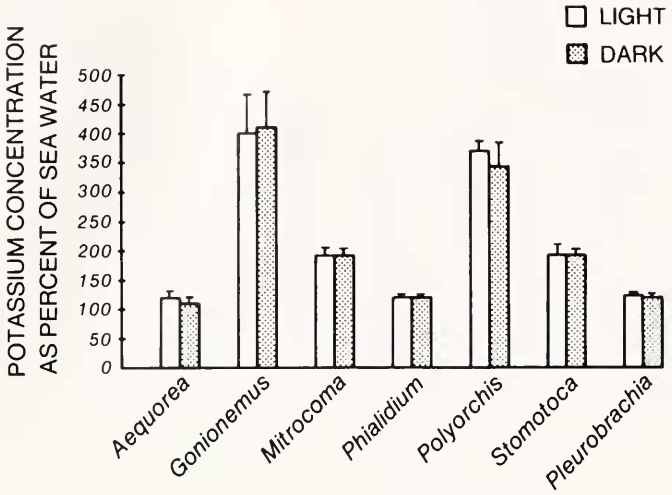

FIGURE 5. Potassium concentrations of 6 species of hydromedusae and 1 ctenophore in the light and dark relative to potassium concentration in sea water. Each bar represents the mean of 5 samples. One standard deviation is indicated above each bar.

coma, and *Aequorea* medusae in a 1500 l aquarium have been observed to gradually change from negative to neutral buoyancy over a period of several days without food (unpub. obs., C.E.M.). This hypothesis has not been systematically investigated.

Although no diel changes in ion levels have been discovered, it seems likely that

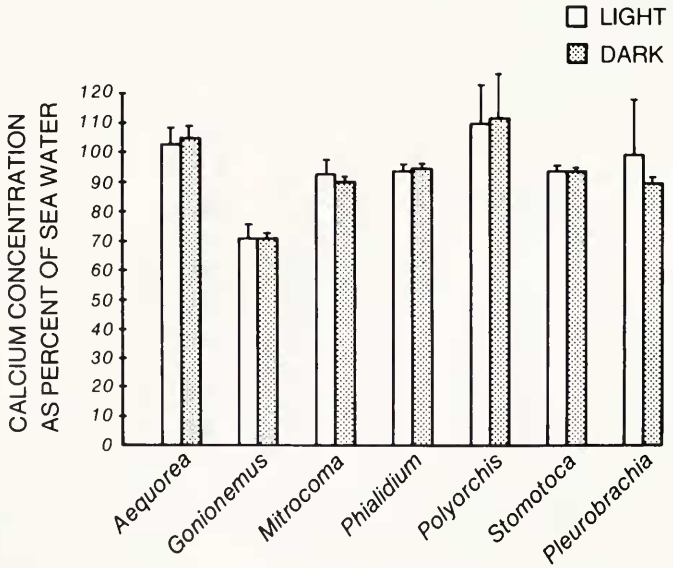

FIGURE 6. Calcium concentrations of 6 species of hydromedusae and 1 ctenophore in the light and dark relative to calcium concentration in sea water. Each bar represents the mean of 5 samples. One standard deviation is indicated above each bar.

continuous exclusion of sulphate is used as a means of obtaining lift perhaps universally by planktonic Cnidaria and ctenophores. Figure 7 summarizes the findings of 8 different papers published over the past 80 years that have reported sulphate concentrations in either whole animals (this study only) or in fluid extracts of the mesogloea. Different techniques for sulphate analysis were used in each study, but in most cases the results are very similar. Mackay (1969) found that no significant sulphate binding occurred in mesogloea and that all of the mesogloeal sulphate ion was exchangeable, so measurements of total sulphate and of labeled sulphate uptake should be comparable. Various authors reported exclusion of 2–92% of the available sulphate in sea water; most of the animals in nature were either neutrally buoyant or slightly negatively buoyant. For most species of pelagic coelenterates and ctenophores, exclusion of sulphate is probably the most important source of lift.

Ammonium ions, when concentrated and retained within tissues, are important in the floatation systems of some marine organisms including dinoflagellates (Singarajah, 1979), tunicate eggs (Lambert and Lambert, 1978), and certain mid-water squid (Denton *et al.*, 1958). Ammonium is present only in very low levels in planktonic Cnidaria and ctenophores (Singarajah, 1979; Bidigare and Biggs, 1980) and apparently makes little contribution to buoyancy in these animals. Some species of hydromedusae (*e.g., Aglantha digitale* and *Plotocnide borealis*) have a relatively large oil droplet that undoubtedly contributes to the buoyancy of these animals, but because these species are not abundant, lipid contributions to buoyancy have not been analyzed in this study. A general review of the various buoyancy mechanisms employed by marine organisms is given by Denton (1963).

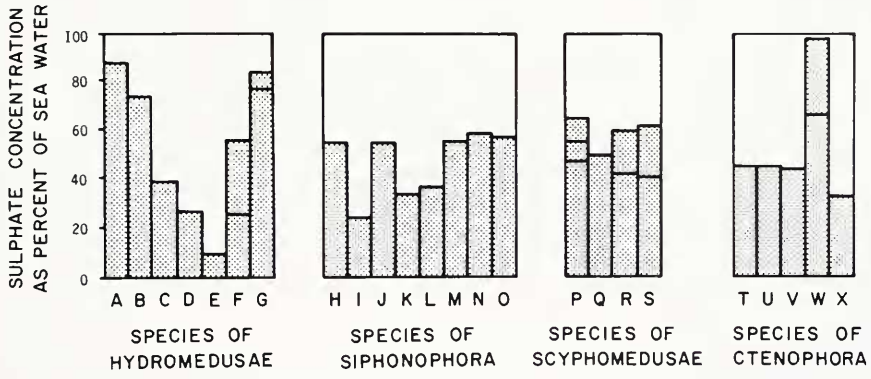

FIGURE 7. Sulphate concentrations of hydromedusae, siphonophores, scyphomedusae, and ctenophores expressed as percent of the sulphate concentration in natural sea water showing concentration in the jellyfishes consistently less than in sea water. Species names and references for sulphate measurements are as follows:

A, *Aequorea coerulescens*[2]; B, *Aequorea victoria* (as *A. aequorea*)[5]; C, *Aequorea aequorea* (as *A. forskalea*)[4]; D, *Aglantha digitale*[8]; E, *Gonionemus vertens*[8]; F, *Mitrocoma cellularia* (also as *Halistaura cellularia*)[5,8]; G, *Phialidium gregarium*[5,8]; H, *Agalma okeni*[7]; I, *Diphyes dispar*[7]; J, *Forskalia edwardsi*[7]; K, *Hippopodius hippopus*[7]; L, *Rosacea cymbiformis*[7]; M, *Stephanophyes superba*[7]; N, *Vogtia glabra*[7]; O, *Vogtia spinosa*[7]; P, *Aurelia aurita* (also as *A. flavidula*)[1,3,7]; Q, *Chrysaora melanaster* (as *Dactylometra pacifica*)[2]; R, *Cyanea capillata* (also as *C. arctica*)[1,2]; S, *Pelagia noctiluca*[4,7]; T, *Beroe cucumis*[7]; U, *Beroe forskalia*[4]; V, *Beroe ovata*[4]; W, *Cestum veneris*[4,7]; X, *Pleurobrachia pileus*[6].

[1] Macallum (1903).
[2] Koizumi and Hosoi (1936).
[3] Robertson (1949).
[4] Denton and Shaw (1962).
[5] Mackay (1969).
[6] Singarajah (1979).
[7] Bidigare and Biggs (1980).
[8] Mills (this report).

The rates of sulphate uptake varied widely in the 6 species examined here (Fig. 1), ranging from less than 4 hours for achieving equilibrium in *Aglantha* to over 75 hours for achieving equilibrium in *Aequorea* and *Mitrocoma.* For species measured in common, our equilibrium times and values are similar to those of Mackay (1969). He interpreted the differences in uptake rate as a reflection of interspecific differences in permeability to sulphate, using specimens of similar sizes so that direct interspecific comparisons could be made. In contrast, we used individuals of different sizes within each species (wet weights ranging nearly 3× in *Mitrocoma* up to 9× in *Aglantha*), yet the intraspecific equilibrium times and values still are fairly constant. This further supports the concept of species-specific sulphate permeability.

Among the other ions measured, potassium exhibits the greatest variation in concentration between species of jellyfish (Figs. 3–6). Because we used whole jellyfish in our study, the high potassium concentrations probably reflect high intracellular potassium, and interspecific differences are presumably indicative of amounts of cellular tissue such as tentacles and gonad relative to the amount of jelly.

Species-specific sulphate concentrations appear to relate loosely to morphology and activity levels, rather than to vertical migration, as originally suspected. For example, *Gonionemus,* which has up to 80 thick tentacles and 4 large gonads (and the greatest potassium concentration), also has the greatest capability for sulphate exclusion. *Gonionemus* is still negatively buoyant, but is a strong swimmer and so can overcome the buoyancy differential. On the other hand, *Sarsia* has only 4 tentacles and a single gonad and is somewhat less efficient at excluding sulphate, yet it achieves positive buoyancy, perhaps because it has less cellular tissue. It appears that hydromedusae have evolved species-specific swimming and feeding patterns based largely on this balance of intrinsic buoyancy and morphology (Mills, 1981).

Buoyancy maintainance that is derived from an active transport system such as the exclusion of sulphate ions or the accumulation of ammonium ions, requires an expenditure of metabolic energy. In the case of tunicate eggs which float due to an accumulation of ammonium ions in follicle cells, Lambert and Lambert (1978) used a variety of metabolic inhibitors to demonstrate unequivocally that the energy for this process comes from glycolysis rather than oxidative phosphorylation. The metabolic basis for ion transport in Cnidaria and ctenophores remains to be determined, as well as the relative energy expenditure for ion pumping *versus* swimming in these organisms.

Acknowledgments

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